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Effects of Ultraviolet-B Irradiances on Soybean.

II. INTERACTION BETWEEN ULTRAVIOLET-B AND PHOTOSYNTHETICALLY ACTIVE RADIATION ON NET PHOTOSYNTHESIS, DARK RESPIRATION, AND TRANSPIRATION[1]

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ABSTRACT

Soybean plants (cv. Hardee) were grown from seed under four ultraviolet-B radiation flux densities and four photosynthetically active radiation levels in a factorial design. Net photosynthesis, dark respiration, and transpiration were measured after 2 and 6 weeks of exposure. Effects of ultraviolet-B radiation were dependent upon photosynthetically active radiation levels. Ultraviolet-B radiation adversely affected net photosynthesis at low photosynthetically active radiation levels, but had little consequence at levels normally saturating photosynthesis in the field. Ultraviolet-B radiation affected both stomatal and nonstomatal resistances to carbon dioxide under low levels of photosynthetically active radiation. The present study demonstrates interactions between ultraviolet-B and photosynthetically active radiation.

Irradiance in the middle UV region has important biological consequences (6, 14). Stratospheric ozone is the principal attenuator of UV radiation reaching the surface of the earth, and it effectively absorbs nearly all of the radiation of wavelengths shorter than 290 nm. Therefore, the naturally occurring portion of the UV-B[3] spectrum at the surface of the earth is between 290 and 320 nm. Natural atmospheric ozone concentrations vary on a diurnal and annual basis and along longitudinal, latitudinal, and altitudinal gradients. Recent attention has also focused on changes in ozone concentration due to human alteration of the atmosphere. These include halogenated hydrocarbons from aerosol propellants, refrigeration systems (8, 17), and solvents (16). These compounds enter catalytic cycles in the stratosphere and may result in lower ozone concentrations. A decrease in atmospheric ozone concentration would result in an enhancement of UV-B radiation reaching the earth's surface. Estimates for potential ozone depletion vary widely, ranging between 6 and 16.5% (11).

Many economically important crop species exhibit reductions in growth and photosynthesis following exposure to UV-B radiation (3–5, 26, 27); however, the mode of action of UV-B radiation on biological systems is not clearly understood. Much of this is a reflection of the wide range of treatment and experimental conditions used by different investigators. Earlier workers used germicidal lamps, which are essentially spectral line-source emitters with a major peak at 253.7 nm (UV-C region), as a UV irradiance source. There is a marked difference between the reactivity of 254 nm radiation and the 290–320 nm wave band in biological systems so conclusions from these earlier investigations must be viewed with caution.

Studies using polychromatic UV-B radiation sources have generally employed UV-B flux densities equivalent to 35–50% ozone depletions (1, 23, 26). Only a few studies have examined the effects of UV-B radiation in lower flux densities and even fewer with high levels of PAR incident during growth (3).

Some of the damaging effects of UV-B radiation are reversible. Photoreactivation is a phenomenon resulting in the repair of UV-B-induced damage and involves the activation of specific enzymes (12, 14). This repair requires simultaneous or subsequent exposure to radiation of longer wavelengths (315–550 nm). Other UV-B modification effects include photoprotection, where biological systems previously exposed to radiation of longer wavelengths show decreased sensitivity to UV-B radiation (6, 12, 14). There is evidence suggesting that UV-B-associated decreases in photosynthesis are photoreactivated or photoprotected (23, 26).

The purpose of the present study was to evaluate the major effects and interactions of four UV-B radiation flux densities on soybeans grown under four PAR levels. More specifically, the objectives were to: (*a*) determine the effects of lower UV-B irradiances on net photosynthesis, transpiration, dark respiration, and the associated diffusive resistances; (*b*) study the relative effects of these UV-B irradiances over a range of PAR levels; and (*c*) examine the validity of extrapolating from experiments conducted in low PAR levels commonly found in greenhouses or growth chambers to field situations.

MATERIALS AND METHODS

Plant Materials and Growth Conditions. Hardee soybeans (*Glycine max* [L.] Merr.), were grown from seed in the controlled environment facilities of the Southeastern Plant Environment Laboratories, Duke University. Seeds were sown in pots containing 250 cm^3 of a 1:1 mixture (v:v) of sand and Vermiculite. These were watered with deionized H_2O and placed in a phytotron greenhouse with a 26/20 C day/night temperature regime. Natural daylight was extended to 16 h by incandescent floodlamps. Soybeans were thinned to two seedlings per pot soon after germination.

Nine replicates in separate pots were grown under each of 16

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[3] Abbreviations: UV-B: ultraviolet radiation between 280 and 320 nm; UV-C: ultraviolet radiation between 200 and 280 nm; UV-B_{BE}: biologically effective ultraviolet-B radiation.

UV-B and PAR treatment combinations. Treatments consisted of four PAR and four UV-B irradiances in a factorial design. UV-B radiation was supplied by stabilizing Westinghouse FS-40 sunlamps. Lamps were preburnt for 100 h prior to use to insure uniformity of UV-B irradiance throughout the course of the experiments. Previous studies have shown lamp aging becomes essentially linear after 100 h of use, with a change of less than 5% total irradiance from approximately 100 to 600 h. Two fixtures, each containing two filtered lamps, were suspended above the plants in each treatment. Radiation from the lamps was filtered by plastic films of either Mylar type S (almost complete absorption of radiation with wavelengths shorter than 320 nm) or 0.076 mm cellulose acetate (transmission of UV-B radiation down to 292 nm). Due to solarization, filters were routinely changed every 3 days to maintain transmission of the desired spectral qualities. The four UV-B irradiances were obtained by matching each lamp with the proper combination of filters and by adjusting the lamp distance above the plants. The distance between the lamps and plants was maintained by raising the lamps as the plants grew.

UV-B irradiances were weighted using two biological action spectra. $UV\text{-}B_{BE}$ is based on the generalized response function for a number of plant action spectra to UV radiation (6). For comparative purposes, these irradiances are also reported after weighting with a UV action spectra for DNA (22). Irradiances used in this study were equivalent to 0 (Mylar control), 17.5, 35.0, and 70.0 effective mw $m^{-2}UV\text{-}B_{BE}$ or 0, 2.39, 4.78, and 9.56 mw m^{-2} of DNA effective radiation. The spectral irradiance corresponding to 35.0 mw m^{-2} $UV\text{-}B_{BE}$ is shown in Figure 1A. Other irradiances were achieved by varying plant to lamp distances (Fig. 1B). On a daily dose basis, the highest irradiance used in this study was similar to that normally incident at Gainesville, Florida (29° 36' latitude) in mid-June during clear sky conditions, when calculated as biologically effective UV-B radiation. The four PAR levels were obtained with neutral density shading materials covering the top and sides of each treatment. Plastic films of Mylar type S separated each treatment to absorb any scattered UV-B radiation. The four shade levels used in the experiment were 0 (unshaded), 33, 55, and 88% shading. Due to the lamp configuration and overhead flowing water used to minimize the effects of shadows, the unshaded or full sun irradiance was slightly lower than field levels, but higher than average greenhouse irradiances. Average maximum daily photon flux density measured at the top of the plants was 1,600 $\mu E\ m^{-2}\ s^{-1}$ PAR. The corresponding average maximum daily PAR flux density under each shade treatment was 1,408, 880, and 528 $\mu E\ m^{-2}\ s^{-1}$, respectively. Leaf temperatures measured with 0.010-mm copper-constantan thermocouples remained at ±3 C of ambient temperature at all PAR levels.

Gas Exchange Measurements. Net photosynthesis, transpiration, and dark respiration were measured at two different UV-B radiation incident doses on single, attached leaves using a cuvette similar to that described by Patterson *et al.* (21). CO_2 was measured in an open system using a Beckman 215B IR gas analyzer and water vapor concentrations were monitored with a Cambridge Systems EG&G model 880 dewpoint hygrometer. All gas exchange measurements were carried out at a leaf temperature of 30 C, ambient CO_2 concentrations of 320 $\mu l/1$, and a vapor pressure deficit of 1 kPa (1 MPa = 10 bar).

Light was supplied by a 120 v, 200 w General Electric cool beam tungsten lamp, filtered through 20 cm water. The photon flux density was varied with neutral density filters producing 1,300, 840, 480 and 170 $\mu E\ m^{-2}\ s^{-1}$ PAR. Photon flux densities in the PAR region were measured at the leaf surface with a Lambda Instruments LI-190S quantum sensor. CO_2 and water vapor fluxes were continuously monitored at each irradiance until equilibration. Dark respiration rates were determined after each series of light response measurements.

Diffusive resistances to water vapor and CO_2 were calculated following conventional resistance analysis (10), using 1.56 as the coefficient relating diffusivities to CO_2 and water vapor (18, 19). Nonstomatal or mesophyll resistances were calculated as a residual term.

Gas exchange measurements were made on soybeans that had received a 6-h/day exposure to UV-B radiation for 14 days (84 h of UV-B radiation accumulation) and 49 days (294 h of UV-B radiation accumulation). UV-B radiation damage also was visually assessed by leaf chlorosis and interveinal wrinkling on a scale ranging between 0 and 9 (Table I). Leaves used in the gas exchange experiments were removed and analyzed for total Chl (2) at the end of the experiment.

RESULTS

Gas Exchange. A photon flux density of 1,300 $\mu E\ m^{-2}\ s^{-1}$ PAR was sufficient to light saturate net photosynthesis in all 16 treatments. Therefore, the effects of UV-B radiation and PAR level during growth on net photosynthesis, transpiration, and the associated diffusive resistances were evaluated at this photon flux density. A separate analysis was done for dark respiration.

A summary of the effects of UV-B radiation on net photosynthesis, transpiration and the associated diffusive resistances after 2 weeks exposure is presented in Table II. On a leaf area basis, net

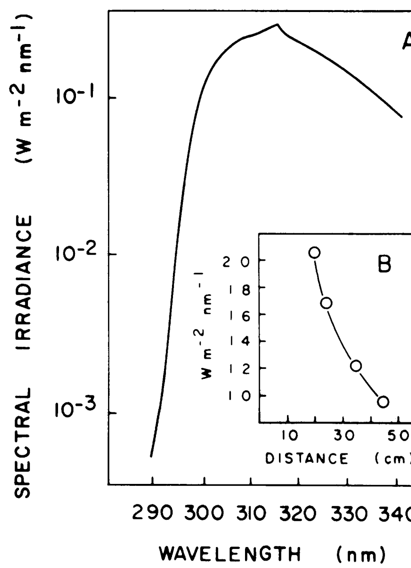

FIG. 1. A: spectrum of UV-B irradiance from two FS-40 lamps filtered by 0.076 mm cellulose acetate. Distance between lamp and spectroradiometer was adjusted to 35.0 mw m^{-2} of biologically effective radiation ($UV\text{-}B_{BE}$). B: relationship of total UV-B irradiance and lamp to plant distance. UV-B irradiance from the 295–340 nm band width provided by two FS-40 lamps filtered through 0.076 mm cellulose acetate.

Table I. *Criteria Used to Rate Degree of UV-B-associated Leaf Chlorosis and Interveinal Wrinkling*

Index of rating	Leaf Chlorosis	Leaf Shape
0	No damage, green leaves	No damage, healthy leaves
2	Yellow leaves present	Very slight wrinkling between leaf veins
4	Yellow leaves with some spots of intense yellow	Interveinal wrinkling
6	Yellow leaves with brown patches	Pronounced interveinal wrinkling
9	Leaf margins dried and curled over, much of leaf dried	Pronounced interveinal wrinkling and leaf curl evident

photosynthesis was significantly reduced in plants grown under a combination of high UV-B radiation and reduced PAR levels. However, net photosynthesis was not significantly affected by UV-B radiation when plants were grown in full sunlight or at lower UV-B radiation flux densities. Similar results were obtained for net photosynthesis calculated on a leaf dry weight basis. Nonstomatal diffusion resistance was unaffected by UV-B radiation in unshaded conditions, but was consistently increased in soybeans grown in reduced PAR levels and 70 mw m^{-2} UV-B_{BE}. Nonstomatal resistances accounted for 80–90% of the total leaf resistance to CO_2 (12–47 cm^{-1} s). Stomatal resistance to CO_2 diffusion accounted for approximately 10–20% of the total leaf resistance, and was greatest in soybeans exposed to 70 mw m^{-2} UV-B_{BE}. Increased stomatal diffusion resistances at the highest UV-B radiation level were reflected in reduced transpiration rates. Dark respiration was not significantly ($P > 0.05$) affected by UV-B radiation.

The cumulative effects of UV-B radiation by the end of 6 weeks resulted in net photosynthesis reductions in all PAR regimes (Table III). These reductions in photosynthesis were directly related to the UV-B radiation accumulated in each treatment. In the lowest PAR level, UV-B flux densities similar to those commonly experienced in the field resulted in decreased photosynthetic rates.

Table II. *Mean Effects of a 2-week Exposure to Four UV-B Irradiances and Four PAR Levels on Net Photosynthesis, Dark Respiration, Transpiration, and Diffusive Resistances in Soybean*

Values in columns for each PAR level followed by same letter are not statistically different at 5% level.

PAR Level	UV-B_{BE}	Net Photosynthesis	Nonstomatal Resistance	Stomatal Resistance	Transpiration	Dark Respiration
% shade	*mw m^{-2}*	*mg CO_2 dm^{-2} h^{-1}*	*s cm^{-1}*		*g H_2O dm^{-2} h^{-1}*	*mg CO_2 dm^{-2} h^{-1}*
0	0	15.9a	13.1a	1.2a	3.8a	2.4a
	17.5	17.2a	13.8a	1.0b	4.2a	1.8a
	35.0	15.7a	12.5a	1.7ab	3.4ab	1.6a
	70.0	15.0a	12.2a	2.4a	2.3b	1.2a
33	0	12.1a	17.3b	1.7b	3.0b	1.0a
	17.5	15.6a	13.1b	1.0b	4.3a	1.1a
	35.0	14.6a	14.3b	1.7b	3.1b	0.8a
	70.0	9.9b	20.2a	2.8a	2.1c	1.0a
55	0	13.1a	16.9b	0.9ab	4.2b	0.6a
	17.5	13.9a	15.6b	0.6ab	5.3a	0.9a
	35.0	15.8a	14.1b	0.9ab	4.3b	0.9a
	70.0	5.5b	47.1a	1.1a	3.9b	1.3a
88	0	12.0a	16.5b	1.0b	4.5a	0.7a
	17.5	11.3a	18.5b	1.1ab	3.8a	0.8a
	35.0	11.0a	18.8b	1.7a	3.1b	0.6a
	70.0	9.3b	23.2a	1.9a	3.4b	0.9a

Table III. *Mean Effects of Four UV-B Irradiances and Four PAR Levels on Soybean Net Photosynthesis, Dark Respiration, Transpiration, and Associated Diffusive Resistances after a 6-week Exposure*

Values in columns for each PAR level followed by the same letter are not statistically different at the 5% level.

PAR Level	UV-B_{BE}	Photosynthesis	Nonstomatal Resistance	Stomatal Resistance	Dark Respiration	Total Chlorophyll	Transpiration
% shade	*mw m^{-2}*	*mg CO_2 dm^{-2} h^{-1}*	*s cm^{-1}*		*mg CO_2 dm^{-2} h^{-1}*	*mg dm^{-2}*	*g H_2O dm^{-2} h^{-1}*
0	0	14.3a	13.2ab	2.8a	1.7a	2.7a	3.9a
	17.5	13.0a	15.1ab	2.1a	1.6a	2.0a	4.7a
	35.0	15.2a	12.3b	2.2a	1.8a	2.6a	4.4a
	70.0	11.6b	16.5a	2.7a	1.3a	2.5a	4.0a
33	0	10.8a	20.7ab	2.3b	0.8a	1.9b	4.4a
	17.5	11.6a	16.0b	2.3b	1.0a	2.0ab	3.4ab
	35.0	11.0a	18.3ab	2.6b	0.9a	2.3ab	3.8ab
	70.0	8.4b	23.2a	4.2a	0.8a	2.5a	2.9b
55	0	10.1a	20.8ab	2.1b	0.6a	1.8a	4.5a
	17.5	10.0a	19.3ab	2.2b	0.4a	1.6a	3.5ab
	35.0	12.1a	16.6b	2.5ab	0.3a	2.2a	3.9b
	70.0	7.9b	25.7a	2.9a	0.6a	1.8a	3.5b
88	0	9.7a	21.9b	1.9b	0.6a	1.3b	4.9a
	17.5	8.3a	25.6b	2.0b	0.5a	1.8a	4.8a
	35.0	7.3b	28.3b	2.7a	0.7a	1.8a	3.7b
	70.0	6.4b	45.2a	3.1a	0.8a	1.7ab	3.6b

Nonstomatal diffusion resistance was significantly affected by UV-B ($P < 0.05$) and PAR ($P < 0.001$), varying inversely with PAR and greatest in soybeans exposed to 70 mw m^{-2} UV-B_{BE}. Stomatal diffusion resistance increased with increasing UV-B radiation flux density, being greatest in those plants exposed to 70 mw m^{-2} UV-B_{BE} (Table III).

Transpiration on a leaf area basis was significantly ($P < 0.05$) reduced after a 6-week exposure to UV-B irradiance. Soybeans grown in moderate to low PAR levels and exposed to UV-B radiation had reduced transpiration rates compared with controls on both a leaf dry weight and area basis. UV-B radiation had little effect on transpiration under unshaded conditions. Reduction in transpiration with increasing UV-B irradiance was reflected in increasing stomatal diffusion resistance. Dark respiration remained unaffected by UV-B radiation exposure.

Total Chl on a leaf area basis was unaffected by UV-B radiation after 6 weeks. Leaf chlorosis and leaf interveinal wrinkling were independent of PAR and directly related to UV-B radiation flux density (Fig. 2). These responses appear to be good indicators of the amount of UV-B radiation received by soybeans regardless of PAR level. Sensitivity of exposures to UV-B irradiance greatly increased between 17.5 and 30 mw m^{-2} UV-B_{BE}, possibly suggesting a threshold effect for these morphological manifestations.

Effects of UV-B radiation incident dose (radiant flux density × exposure time) on net photosynthesis in soybeans grown in contrasting PAR levels are shown in Figure 3. Greater UV-B radiation accumulation resulted in larger reductions in photosynthesis. The effects of incident dose were dependent upon the PAR level during UV-B radiation exposure. Soybeans grown in higher PAR levels accumulated larger UV-B radiation doses before reductions in photosynthesis occurred.

DISCUSSION

The combined effects of UV-B radiation and PAR on net photosynthesis and the diffusive resistances to CO_2 and water vapor demonstrated the importance of longer wavelength radiation in determining the degree of UV-B alteration of normal plant processes. Soybeans exposed to UV-B radiation and grown in unshaded conditions in the phytotron did not show a reduction in net photosynthesis until 6 weeks of accumulation. However, net photosynthesis was immediately affected by high UV-B irradiances in reduced PAR levels. Soybeans exposed to 70 mw m^{-2} UV-B_{BE} resulted in a 23% reduction in photosynthesis under shaded conditions.

These reductions were primarily due to increases in nonstomatal (mesophyll) diffusion resistance. This large resistance term includes resistances associated with carboxylation and excitation in photosynthesis (13, 19). Other evidence indicates UV radiation exposure results in an inhibition of PSII and to a lesser extent PSI of photosynthesis (5, 15, 20, 27, 28). This may be associated with UV-B-induced disruption of the structural integrity of the lamellar membrane systems in the chloroplasts (5, 7, 15). Total leaf Chl was unaffected by the range of UV-B irradiances used in the present study. Therefore, the reduction in net photosynthesis in irradiated plants was not an indirect effect due to inhibition of Chl synthesis or Chl destruction.

Decreased sensitivity to UV-B radiation damage may result from photoreactivation or photoprotection (6, 12, 14). There is evidence suggesting the damaging effects of UV-B radiation on a large number of physiological phenomena, including reductions in net photosynthesis, might be reversed by radiation at longer wavelengths (9, 23, 25, 26). The data presented here support this hypothesis. Net photosynthesis in high PAR levels was nearly unaffected throughout the range of UV-B irradiances tested. However, as light became limiting to photosynthesis, the damaging effects of UV-B increased.

These findings are somewhat different from those reported by Sisson and Caldwell (23) where *Rumex patientia* L. was grown under ambient PAR levels in the field (maximum PAR was 2,100 $\mu E\ m^{-2}\ s^{-1}$), and 800 and 400 $\mu E\ m^{-2}\ s^{-1}$ in controlled environment chambers. They noted large reductions in net photosynthesis in all three PAR regimes due toUV-B radiation enhancement. However, the maximum UV-B irradiance used in the *Rumex* study corresponded to an ozone depletion of 38%, compared to the ambient mid-June levels in the present study. The deleterious effects of UV-B radiation were magnified by low PAR growth conditions and a high UV-B irradiance.

Sisson and Caldwell (24), extrapolating from a *Rumex*-based model, reported that even low UV-B irradiances result in reductions in net photosynthesis over time due to reciprocity. Decreasing

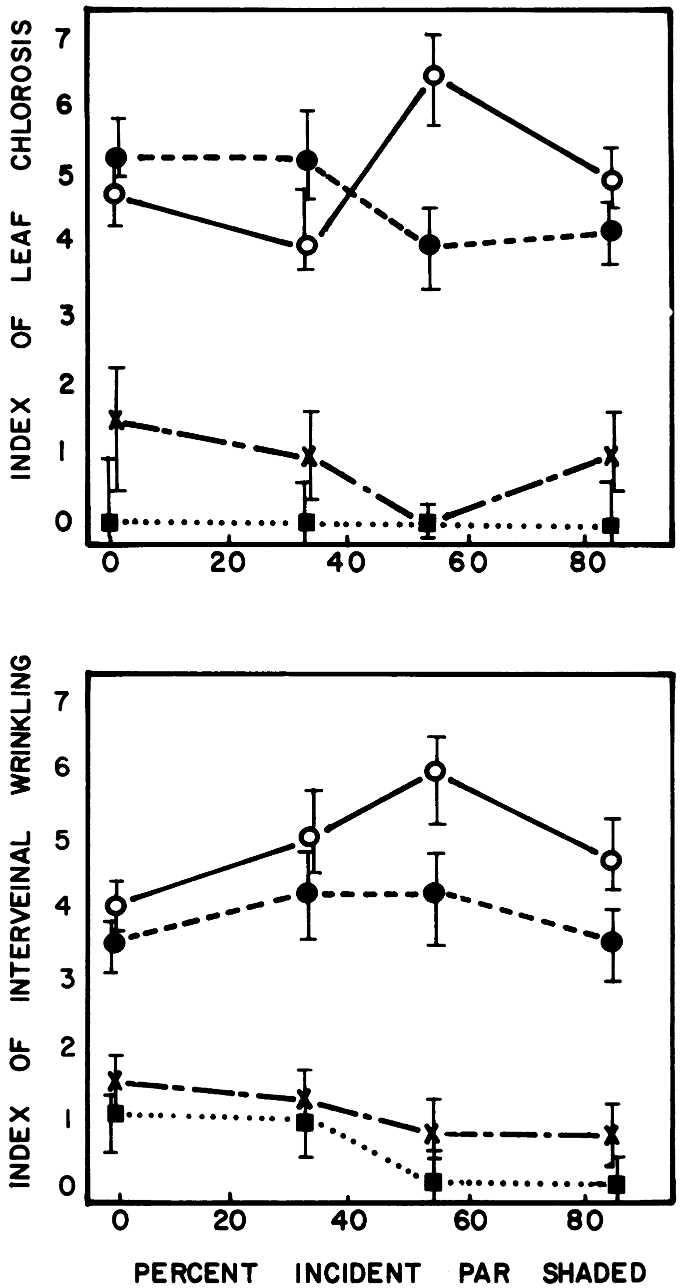

FIG. 2. Indices for interveinal leaf wrinkling and leaf chlorosis observed after 6 weeks of treatment. Each point represents mean of nine observations and vertical bars represent ±1 SD. Sixteen treatments were a combination of four UV-B and four PAR flux densities. (■): Mylar control; (×): 17.5 mw m^{-2} UV-B_{BE}; (●): 35.0 mw m^{-2} UV-B_{BE}; (○): 70.0 mw m^{-2} UV-B_{BE}.

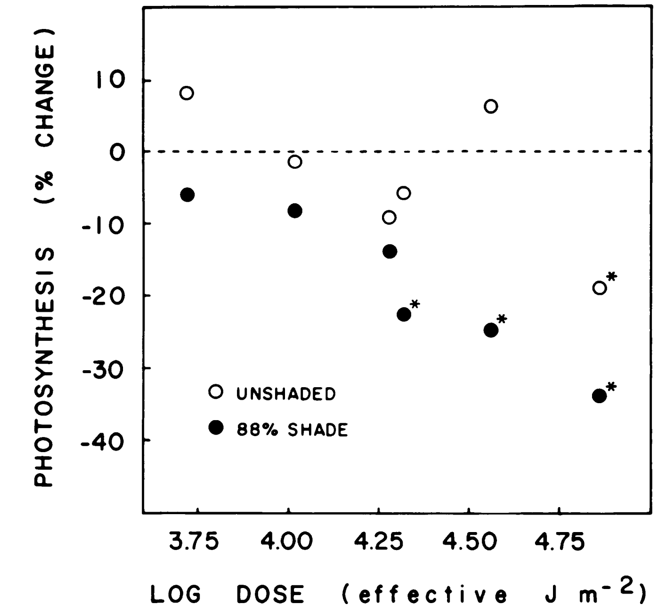

FIG. 3. Effects of log UV-B radiation incident dose on per cent change of net photosynthesis from controls in soybeans under two levels of shade. Each point represents the mean of four observations. Values above the dashed horizontal line indicate enhancements; those below it indicate reductions. Asterisks indicate values significantly ($P < 0.05$) less than control.

net photosynthesis and transpiration rates during the 6 weeks of UV-B radiation exposure in the present study demonstrate that soybeans are increasingly affected by increasing UV-B radiation incident dose. Effects of leaf age were not tested, and may have also contributed toward increased leaf diffusion resistance. These data further suggest that reciprocity possibly occurs at lower UV-B radiation incident doses under reduced PAR levels. Equivalent reductions in net photosynthesis required a greater incident dose in full sunlight than in 88% shade, possibly attributable to longer wavelength repair mechanisms at high PAR irradiances (Fig. 3).

Two indices, interveinal leaf wrinkling and leaf chlorosis, demonstrated threshold effects. Low irradiances (17.5 mw m^{-2} UV-B_{BE}) had no effect on either symptom; however, exposure to 35 and 70 mw m^{-2} UV-B_{BE} greatly affected both. The precise nature of these morphological responses might be quite complex, but they were independent of PAR, suggesting they were irreversible. Alternatively, the repair mechanisms operating on these reponses might be light-saturated at very low levels. Interveinal wrinkling and leaf chlorosis were observed only if leaves were exposed to UV-B irradiances from early leaf expansion to maturity. Fully expanded leaves exposed to high UV-B irradiances (up to 150 mw m^{-2} UV-B_{BE}) did not develop either manifestation (data not shown). Therefore, interveinal wrinkling is the result of UV-B effects on cell division or expansion early in leaf development. Sisson and Caldwell (23) similarly argued that leaf expansion is affected more during the initial exposure to UV-B radiation.

Campbell (7) found chloroplasts appeared to be the first organelle to show injury responses when soybean leaves were irradiated with UV-B radiation. Much of this injury was similar to that found in the final stages of leaf aging. Leaf chlorosis was manifested only in leaves which had expanded in UV-B radiation and not in fully expanded mature leaves, hence these data indicated UV-B radiation might be interfering with normal proplastid differentiation, rather than an acceleration of leaf senescence.

Dark respiration rates were unaffected by UV-B radiation even after 6 weeks exposure. It was not clear whether this was due to repair phenomena or if dark respiration was simply unaffected by the UV-B irradiances employed. Sisson and Caldwell (23) reported increased dark respiration rates in *Rumex* after only a few days of exposure. However, that study incorporated a much higher UV-B radiation flux density and relatively low PAR levels.

It has been shown here that low UV-B irradiances (even less than naturally occurring in the field) had an effect on photosynthesis. Larger UV-B radiation flux densities or greater accumulated doses resulted in greater photosynthetic reductions. Both stomatal and nonstomatal diffusive resistances were affected by UV-B radiation. Stomatal effects were also reflected in reduced transpiration rates. These data suggest the general repair of UV-B-induced damage to net photosynthesis was ineffective at low PAR levels, but may have played an important role in unshaded, ambient situations. Soybean net photosynthesis was unaffected by irradiances up to 70 mw m^{-2} UV-B_{BE} when grown for 2 weeks in unshaded conditions. Additionally, our study revealed that plant responses to various combinations of UV-B irradiances and PAR levels are complex. Soybean response to increasing UV-B irradiance was dependent upon the level of incident PAR. Consequently, interpretations of growth chamber or greenhouse studies regarding the effectiveness of moderate UV-B irradiances in natural situations must be viewed with caution.

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